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Microwear evidence for Plio–Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa

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Abstract

Makapansgat Limeworks Cave is a well-known *Australopithecus africanus* bearing locality that has spawned a considerable amount of paleoecological research because of its hominin component. Most recently, the paleoecology of this Plio–Pleistocene site has been studied by determining the diet and habitat of other extinct taxa, particularly the bovids. The diets of seven bovids (*Aepyceros* sp., *Gazella vanhoepeni*, *Makapania broomi*, *Parmularius braini*, *Redunca darti*, *Tragelaphus* sp. aff. *T. angasii*, and *Tragelaphus pricei*) have now been classified using taxonomic uniformitarianism, ecomorphology, stable carbon isotopes, and mesowear analysis. Here, dental microwear is applied to the same bovids for additional comparison and to further elucidate the strengths and weaknesses of each method. The different dietary proxy methods noted provide a temporal continuum, with genetic signals such as ecomorphology and taxonomic uniformitarianism indicating behavioral adaptations over geologic time, while nongenetic data such as stable carbon isotopes and mesowear reflect different aspects of average diet over extended portions of an animal's life, and dental microwear provides dietary snapshots.

Microwear separated an extant baseline of ten bovid species into expected dietary categories and the Makapansgat bovids clearly fell into two groups with the same degree of separation as between extant grazers and browsers. The results indicate that a multidisciplinary approach produces a more accurate and robust reconstruction of past diets. In sum, the microwear analysis is in-line with the isotope and mesowear results, which suggest a stronger browsing component than either taxonomic uniformitarianism or ecomorphology imply.

Keywords: Plio–Pleistocene; Bovids; Microwear; Paleodiets; Paleoecology; Makapansgat

1. Introduction

Mammalian paleoecology has traditionally focused on taxonomic uniformitarianism. This method is based on the assumption that fossil taxa evince the ecological preferences of their closest living relatives. While this technique is certainly of some value in analyzing

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relatively recent faunas, its utility in determining the paleoecology of extinct taxa is questionable. The main problems with this method are that it requires taxonomic groups to remain ecologically constant through time and it provides little or no information about extinct forms with no living relatives (Sponheimer et al., 1999).

A number of techniques have been developed in recent years that take a more empirical approach to dietary reconstruction, such as (1) ecomorphology, or morphological studies that reflect long-term ecological adaptations (e.g., Janis, 1988; Janis and Fortelius, 1988; Solounias and Moelleken, 1993a,b; Solounias et al., 1995; Spencer, 1995; Reed, 1996), (2) stable carbon isotopes (e.g., Aufderheide, 1989; Lee-Thorp et al., 1989; Sponheimer et al., 1999; Ambrose and Katzenberg, 2000; Lee-Thorp and Sillen, 2001), (3) dental microwear, the study of short-lived microscopic wear patterns on teeth (e.g., Solounias et al., 1988; Teaford, 1988a,b; Solounias and Moelleken, 1993b; Solounias and Hayek, 1993; Rose and Ungar, 1998; Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Merceron et al., 2004a,b), and (4) dental mesowear, the study of cusp wear patterns over an extended period of an animals lifetime (e.g., Fortelius and Solounias, 2000; Kaiser et al., 2000; Franz-Odendaal, 2002; Kaiser and Solounias, 2003; Kaiser and Fortelius, 2003; Franz-Odendaal and Kaiser, 2003; Franz-Odendaal et al., 2003; Schubert, in press). Researchers have also combined some of these techniques showing that multiple methods result in more solid paleodietary reconstructions (e.g., Solounias and Moelleken, 1993b; MacFadden et al., 1999; Sponheimer et al., 1999).

A great deal of research has focused on reconstructing the environment of Makapansgat. Methods for interpreting the paleoenvironment of the site have ranged from pollen analysis (Cadman and Rayner, 1989; Rayner et al., 1993; Zavada and Cadman, 1993) to taxonomic uniformitarianism (e.g., Wells and Cooke, 1956; Vrba, 1982) and ecomorphology (Reed, 1996, 1998). More recent work has focused on testing taxonomic uniformitarianism of bovids by comparing these results to ecomorphology and stable carbon isotopes (Sponheimer et al., 1999). This interdisciplinary study led Sponheimer et al. to suggest that two taxa (*Aepyceros* sp. and *Gazella vanhoepeni*), previously thought to be mixed feeders based on taxonomic uniformitarianism and ecomorphology, were in fact browsers.

This paper expands on the work of Sponheimer et al. (1999) by adding an additional proxy measure of diet for the same seven bovid taxa, dental microwear. The primary objectives of this project are: (1) to conduct dental microwear on an extant baseline of bovids with known diets and compare these results with the dental microwear of the Makapansgat bovids, grouping the fossil taxa into dietary categories, and (2) to compare the dietary classifications based on microwear, mesowear (Schubert, in press), stable carbon isotopes, ecomorphology, and taxonomic uniformitarianism for the seven Makapansgat bovids and address the importance of these results for paleoecology.

2. Makapansgat

Makapansgat Limeworks Cave (24°12′S, 29°12′E) is located northeast of Johannesburg some 15–20 km east–northeast of the town of Mokopane in the Makapansgat Valley, Limpopo Province, South Africa. Member 3 is the main fossil bearing unit at Makapansgat and dates to about 2.5–3.2 Ma based on biostratigraphic (Harris and White, 1979; Vrba, 1982; Delson, 1984) and paleomagnetic evidence (Partridge, 1979; Partridge et al., 2000; Herries, 2003). The faunal assemblage is extensive and diverse, consisting of bats, insectivores, anteaters, baboons, hominins, saber-toothed cats, hyenas, hyraxes, elephants, horses, rhinos, hippos, pigs, antelopes, giraffes, chalicotheres, and porcupines and other rodents (Maguire et al., 1980; Reed, 1996). At least 60% of the craniodental material is from bovids (Reed, 1996) and over two-thirds of the mammalian species are extinct (McKee, 1995). Makapansgat is one of several localities to contain *Australopithecus africanus* remains (Tobias, 2000) and is considered by some to be the oldest hominin bearing site in South Africa (McKee, 1995, 1999; Vrba, 2000).

Environmental reconstructions for Makapansgat are numerous and quite varied (e.g., Rayner et al., 1993; Reed, 1998; Latham et al., 1999; Sponheimer et al., 1999; McKee, 1999). These interpretations range from open desert to closed forest (Rayner et al., 1993). Both Cadman and Rayner (1989) and Rayner et al. (1993) suggested, for example, that the site was a forest based on pollen. However, McKee (1999) points out that these palynological analyses may be erroneous based on the inclusion of modern exotics in the sampled sediments. While it may not have been a true forest, the faunal composition from Members 3 is consistent with a woodland environment (Reed, 1996) because it is composed of a high percentage of browsers. The co-occurrence of grazers and species like the cheetah suggest the area was more of a mosaic and open grassy habitats existed as well (McKee, 1999). When compared to the other hominin-bearing South African Plio–

Pleistocene sites Makapansgat appears to have been the most densely vegetated.

3. Bovid diets and paleodiets

Bovids are often used as paleoenvironmental indicators because they are common in many Plio–Pleistocene fossil assemblages and can be readily separated into general dietary categories that reflect habitat preferences (e.g., Sponheimer et al., 1999). These conventional dietary categories reflect the percentages of monocotyledons (monocots) and dicotyledons (dicots) in their diets. The categories are (1) grazers, those species that eat mostly monocots and typically occur in more open habitats, (2) browsers, those that eat mostly dicots and tend to occur in more densely vegetated habitats, and (3) mixed feeders, a large intermediate category of taxa that alternate their diets seasonally or regionally between grazing and browsing (Fortelius and Solounias, 2000).

It is well known that bovid diets are considerably more complex than the three dietary groupings suggest, and there are numerous intermediate categories that exist (for review see Gagnon and Chew, 2000). Nevertheless, separating taxa into the three traditional dietary groups has proven to be a useful method for interpreting the paleodiets and paleoenvironments of extinct species (Janis, 1988; Fortelius and Solounias, 2000; Merceron et al., 2004a,b).

4. Dental microwear

The analysis of microscopic wear features on teeth (dental microwear) is considered to be one of the most effective ways of inferring the diets of past vertebrates. Dental wear is the result of abrasion and attrition. In bovids and other artiodactyls, chewing takes place in a one-phase upward and inward occlusal motion. This produces an occlusal surface that is relatively straight labio-lingually. Chewing of this type, also called translatory chewing, requires differential width of upper and lower teeth (anisodonty) so that one tooth row moves across the other while maintaining occlusal contact (Rensberger, 1973; Fortelius, 1985; Franz-Odendaal and Kaiser, 2003).

Different types of foods have differing material properties and shapes. Therefore, mastication of varying food types requires somewhat different strategies of occlusion. For example, grasses are tough and relatively thin. Bovids process grasses in the mouth by extreme lateral motion, that is, the lower teeth primarily move laterally across the upper teeth in a cyclical pattern. This results in abrasion of teeth caused by the grinding action of hard food particles such as phytoliths and grit across the occlusal surfaces (Rensberger, 1973; Franz-Odendaal and Kaiser, 2003). At a microscopic level, such interaction results in linear features (or scratches) primarily oriented labio-lingually.

Browsers on the other hand consume foods that (1) have more variation in size and shape, (2) likely have less adherent grit, and (3) are not as concentrated in phytoliths and the phytoliths are much smaller (McNaughton et al., 1985). Larger objects, such as nuts and seeds, are brittle and require some vertical pressure for breaking. However, because such foods do not contain the same concentration or size of phytoliths as grasses, they cause less abrasion (or higher attrition) of teeth. Instead, a browsing diet results in teeth that have higher percentages of microscopic pits than found for grazers. Different sized pits may have different etiologies (Teaford and Oyen, 1989a,b; Teaford and Runestad, 1992). For example, larger pits are thought to be the result of concentrated pressure on hard food items between enamel surfaces (puncture crushing), and small pits may be due to strict tooth–tooth wear (Walker, 1984; Teaford and Oyen, 1989a,b; Teaford and Runestad, 1992). When tooth–tooth contact occurs, it is actually at relatively small focal areas of the occlusal surfaces, thus high pressures are exerted at microscopic points on the enamel (Teaford and Runestad, 1992). The effect of this may be either adhesive wear due to welds occurring between prisms on opposing teeth, resulting in the transfer of enamel from one surface to another, or microscopic fracturing of prisms at prism boundaries. Both of these would cause small prism-sized pits (Teaford and Runestad, 1992). Walker (1984) referred to this process of prism-sized pit development as prism plucking.

An understanding of relationships between diet and microwear patterning in extant species has allowed researchers to infer feeding behaviors from microwear patterning in a broad range of fossil taxa (Rose and Ungar, 1998). Bovid studies have thus far shown that most modern grazers and browsers can be differentiated by dental microwear features, with grazers having more scratches and browsers having more pits (Solounias and Hayek, 1993; Solounias et al., 1988; Merceron et al., 2004a,b). However, mixed feeders can have microwear patterns similar to those of grazers and browsers, making it difficult to exclude mixed-feeding as a dietary preference based on microwear alone (Solounias and Hayek, 1993; Solounias et al., 1988, 2000). Unfortunately microwear techniques for bovids and other taxa vary widely in methodology and magnification and most analyses are not directly comparable.

5. Materials and methods

For the extant bovid baseline analysis, casts of upper and lower second molars of wild caught museum specimens were used (Table 1). The dental molds from these specimens were collected from the American Museum of Natural History (AMNH), New York, the Harvard Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts, the South African Museum (SAM), Cape Town, and the Transvaal Museum (TM), Pretoria. The sampled extant taxa were chosen because they vary widely in ecological preferences, with diets and habitats ranging from desert adapted dry grass grazers (*Oryx gazella*), to fresh grass grazers (*Redunca arundinum*), to specialized browsers (*Litocranius walleri*) (Hofmann and Stewart, 1972).

The Makapansgat (M) Member 3 fauna is curated at the Bernard Price Institute for Paleoecological Research (BPI), Johannesburg, South Africa. Molds were made of selected bovid specimens (Table 2) at the BPI in June of 2002. All available specimens were examined and most showed postmortem damage so had to be excluded. In addition, excessively worn and unworn teeth were excluded from the analysis. Most of the teeth used were upper and lower second molars, which have been shown in other studies to yield comparable results (Merceron et al., 2004a,b). However, in a few cases, lower first molars were used to increase sample sizes of the extinct taxa.

Table 2
Makapansgat bovids included in this study and the number of specimens used for each

Taxon (code)	*N* cast M2/m2s	*N* used M2/m2s	*N* used m1s	Total *N* used
Tragelaphus sp. aff. *T. angasii* (tSAA)	7	5	1	6
Tragelaphus pricei (tP)	7	4	0	4
Redunca darti (rD)	57	12	0	12
Gazella vanhoepeni (gV)	21	7	1	8
Aepyceros sp. (aS)	12	2	0	2
Parmularius braini (pB)	10	3	2	5
Makapania broomi (mB)	35	4	3	7

N cast=number of specimens cast, *N* used=specimens that preserved antemortem microwear and were used in this analysis.

High-resolution casts were prepared following conventional microwear procedures. The casting procedure is described in detail elsewhere (Rose, 1983; Grine, 1986). Original specimens were cleaned with acetone and alcohol soaked cotton swabs, and then impressions were taken using a polyvinylsiloxane dental impression material ("President Jet Regular", Coltene/Whaledent Corp.). Casts were made using a high-resolution epoxy polymer (Epotek, Epoxy Technologies, Inc.). This procedure has been shown to produce stable replicas that consistently and reliably reproduce features with a resolution to a fraction of a micron (Beynon, 1987; Teaford and Oyen, 1989b).

Table 1
Modern bovids examined using microwear analysis and the associated diet of these species

Taxon (code)	Common name	*N*	Diet
Grazers			
Connochaetes taurinus (ct)	Wildebeest	10	Short grass grazer
Damaliscus dorcas (dd) (subspecies *D. d. phillipsi*)	Blesbok	10	Relatively pure grazer
Hippotragus niger (hn)	Sable	8	Grasses in rainy season, grasslands in dry season in search of green plants, including forbs and foliage
Oryx gazella (og)	Oryx	10	Close cropping of coarse desert grasses. Browses to some extent, and digs for roots, bulbs and tubers.
Redunca arundinum (ra)	Common Reedbuck	11	Drainage-line grassland; grazer but will eat forbs and browse woody vegetation in dry season; tall grass specialist
Mixed feeders			
Gazella thomsoni (Gt)	Thomson's Gazelle	9	Grazes on green tender grasses, supplementing diet with green browse
Aepyceros melampus (Me)	Impala	7	Grazer when grasses are green and browser of foliage, forbs, shoots, and seedpods at other times
Tragelaphus scriptus (Ts)	Bushbuck	11	Herbs, leguminous plants and new green grass
Browsers			
Litocranius walleri (LW)	Gerenuk	7	One of the purest browsers; mostly leaves and flowers of shrubs and trees
Tragelaphus strepsiceros (TS)	Greater Kudu	14	Nearly pure browser, leaves, herbs, fruits, succulents, vines, tubers, flowers

Diet descriptions compiled from the following references (Stewart and Stewart, 1970; Jacobsen, 1974; Leuthold, 1978; Estes, 1991; Murray, 1993; Kingdon, 1997; Fortelius and Solounias, 2000; Gagnon and Chew, 2000).

A NanoSurf II Pro (Solarius Corp.) white light scanning confocal microscope was used for image analysis. This microscope allows the generation of images comparable in clarity and resolution to typical dental microwear photomicrographs produced by scanning electron microscopy without the need to coat replicas, or place them in an evacuated chamber (Ungar et al., 2003). The study focused on shearing facets of upper and lower second molars (Fig. 1). These two surfaces are in contact during chewing, thus these teeth are combined into a single sample (Teaford and Walker, 1984). Surfaces were checked for postmortem damage using procedures detailed elsewhere (Teaford, 1988a,b; King et al., 1999), and only those that preserved unobstructed antemortem microwear were included in this analysis. Of the fossil teeth replicated at the BPI, only a small percentage preserved antemortem dental microwear features.

Occlusal enamel surfaces were examined at a resolution of 0.6 μm per pixel, yielding a field of view that was approximately 300 μm × 300 μm with a 512 × 512 pixel array. Depth data for each pixel were leveled and converted to an image by photorealistic shading in the Nanosurf software package. Pseudo lighting parameters used to define the image were kept constant with an azimuth (alpha) of 0° and a declination (beta) of 30–40°. This produces a pseudophotomicrograph indistinguishable from that produced using comparable fixed stage to collector geometry. Screen captured images were saved as bitmap files for analysis. Codes were given to each taxon, and images were placed in coded files prior to microwear analysis. These codes were given to remove the possible bias involved in quantifying features for species with known or presumed diets. Examples of microwear images for most of the analyzed taxa are shown in Fig. 2.

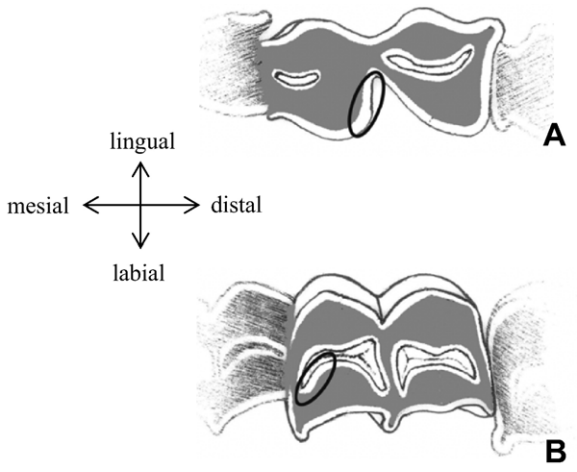

Fig. 1. Shearing facets where microwear was examined on bovid second molars (drawings courtesy of Gildas Merceron). A = left m2, B = RM2.

One field of view was analyzed for each specimen examined. Microwear features were identified and measured using Microware 4.02 (see Ungar et al., 1991; Ungar, 1995). A mouse-driven cursor was used to delineate four points per feature which define the length (major axis) and width (minor axis). After features were identified, the software automatically computed summary statistics for each specimen. Statistics considered in this study include (1) average pit percentages; (2) average pit width; (3) average scratch width; (4) average lengths of the mean striation orientation vectors (r); and (5) the average length of minor (feature width) and major axes (feature lengths). Appendix II in Schubert (2004) provides a list of specimens used from each species as well as statistical data for each specimen.

A pit is defined as a feature that has a length ≤ four times its width while a scratch has a length > than four times its width (Grine, 1986). The pit percentage or percentage incidence of pitting is calculated by dividing the total number of pits by the total number of features. Orientation vector lengths measure how homogeneous the orientations of the long axes are relative to a fixed angle. This measurement ranges from $r = 0$ (orientation of major axes distributed evenly) to $r = 1$ (orientation of all major axes are the same).

Microwear feature patterns on images were quantified using techniques similar to those described by Ungar (1995, 1996; Ungar et al., 1991). Because distribution normality and homogeneity cannot be assumed for the microwear feature data, these data were rank transformed for statistical comparisons. This is a conservative method that provides a link between parametric and nonparametric statistics. Ranking data allows the assessment of interactions among factors and permits multiple comparison tests that are not available with conventional nonparametric methods (Conover and Iman, 1981).

To determine whether the bovid taxa varied significantly from one another in overall shapes and features sizes, a multivariate ANOVA (MANOVA) was used to analyze microwear feature dimensions. In this analysis, taxon was the dependent variable (with measurement means for each as the replicate) and minor and major axis lengths were the independent variables. One-way ANOVAs on each of the microwear features were used to determine the sources of significant variation. Bonferroni's pairwise comparisons were using to assess whether significant differences existed between taxa for each of these microwear feature dimensions.

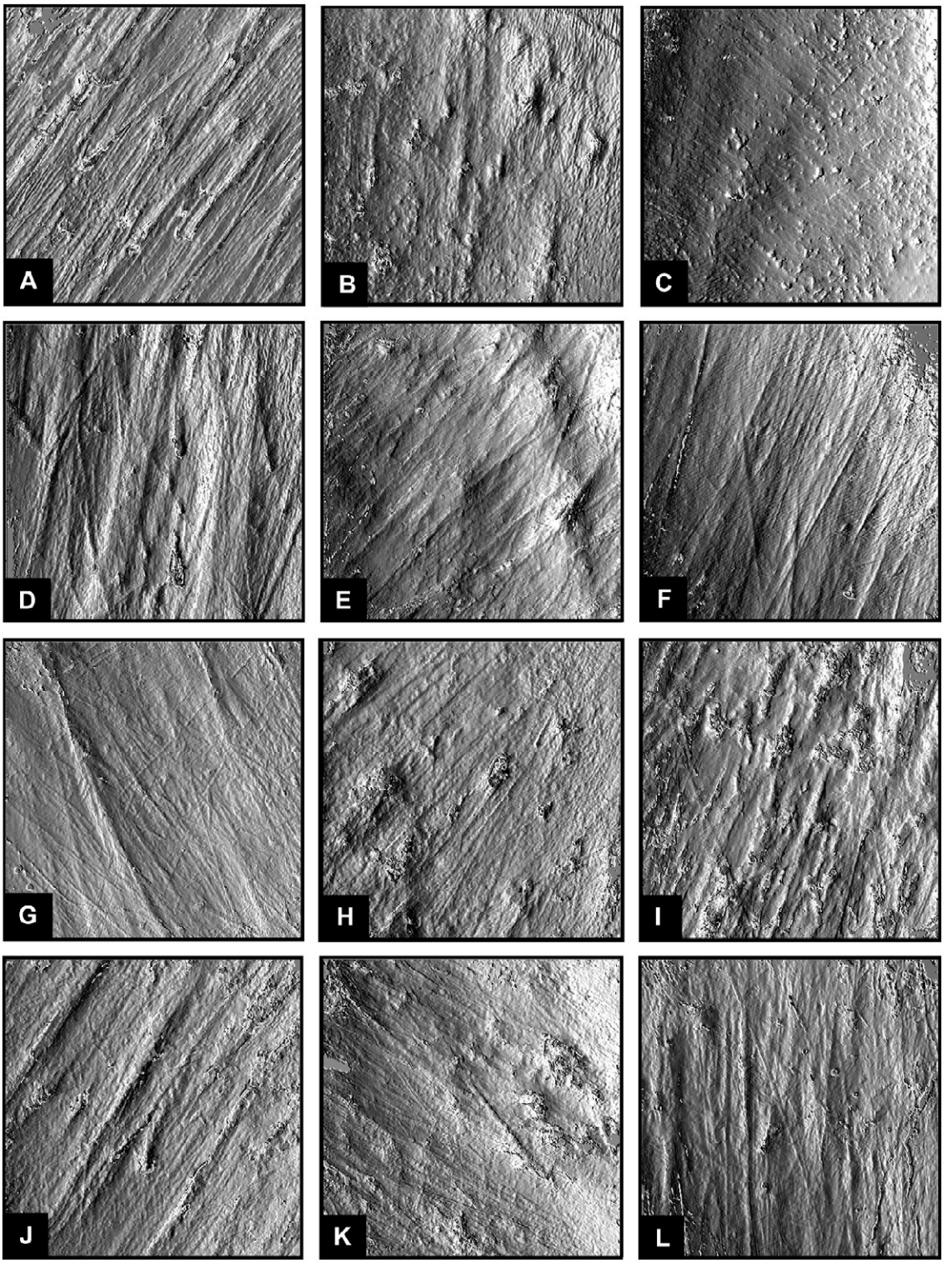

Fig. 2. Microwear images of extant African bovids (A–E) and extinct bovids from Makapansgat (F–L); (A) *Tragelaphus scriptus* (TM38914); (B) *Tragelaphus strepsiceros* (TM16601); (C) *Litocranius walleri* (MCZ 8734); (D) *Connochaetes taurinus* (AMNH81794); (E) *Redunca arundinum* (AMNH80506); (F) *Redunca darti* (M879); (G) *Parmularius braini* (M777); (H) *Tragelaphus* sp. aff. *T. angasii* (M9018); (I) *Tragelaphus pricei* (M133); (J) *Aepyceros* sp. (M9177); (K) *Gazella vanhoepeni* (M42); (L) *Makapania broomi* (M7112). Images 300 × 300 μm.

6. Results

A total of 141 specimens from seventeen species were analyzed for dental microwear. Statistical analyses of these results are presented in Tables 3 and 4, and Appendix A.

6.1. Pit percentage

The taxa varied widely in their ratios of pits to scratches on enamel bands (Fig. 3). For extant taxa the mean for pit % ranged from 24.6% in *Oryx gazella* to 92.5% in *Litocranius walleri*. For the extinct taxa, these values ranged from 16.3% in *Redunca darti* to 41.9% in *Tragelaphus* sp. aff. *T. angasii*. The obvious separation between extant taxa is between the browsers and grazers, with browsers having considerably higher mean pit percentages. The extinct bovids fall into two groups: (1) those with higher pit percentages that overlap with some extant grazers and mixed feeders, and (2) those that had low pit percentages — lower than any of the extant grazers. Because of the small sample size for *Aepyceros* sp., differences between it and other taxa are not evaluated statistically.

Statistical analysis showed significant variation in the model among the taxa (Table 4). Subsequent pairwise comparisons indicated that most taxa differed significantly from other taxa in the data set (Appendix A). For example, three extant grazers (*Connochaetes taurinus*, *Redunca arundinum*, and *Oryx gazella*) and one mixed feeder (*Tragelaphus scriptus*) had significantly lower pit percentages than two browsers (*Tragelaphus strepsiceros* and *Litocranius walleri*) and one of the mixed feeders (*Gazella thomsoni*). *Gazella vanhoepeni*, *T. pricei*, and *T.* sp. aff. *T. angasii* have significantly higher mean pit percentages than *R. darti*, *P. braini*, and *M. broomi*. In fact, these three latter taxa have significantly lower pit percentages than most of the extant taxa, including three of the grazing taxa (*H. niger*, *R. arundinum*, and *D. dorcas*).

6.2. Pit width

Mean pit widths did not vary much, with mean values ranging from 3.8 to 5.7 μm for all the taxa (Fig. 4). Clear exceptions to this in the extant taxa are *C. taurinus* which has wider pits on average than *H. niger* and *O. gazella*. For the fossil material, *G. vanhoepeni* stands alone in having a relatively small average pit width compared to the other fossil taxa and to all the compared extants.

Table 3
Multivariate analysis of variance results for major and minor axes considered together

Test	Statistic	*F*	*df*	*P*
Wilks' Lambda	0.147	12.346	32, 246	0.000
Pillai Trace	1.187	11.308	32, 248	0.000
Hotelling–Lawley Trace	3.523	13.432	32, 244	0.000

While within-group variation in pit widths was considerable, statistical analysis still revealed significant variation among the taxa (Table 4) and pairwise comparisons showed that some of the taxa were significantly different from one another (Appendix A). The mean pit width of *C. taurinus* was significantly wider than two other grazers, *D. dorcas*, *H. niger*, and the mixed feeder *O. gazella*. The extinct gazelle, *Gazella vanhoepeni* had a significantly lower mean pit width than *M. broomi* and *R. darti*.

6.3. Scratch width

Mean scratch widths for the extant taxa ranged from 2.4 μm in *Oryx gazella* to 3.4 μm in *Litocranius walleri* (Fig. 5). For some of the taxa (e.g., *L. walleri*), within-species variation was extreme. *Connochaetes taurinus* had a wider scratch width on average than the other grazers. For the extinct taxa, *G. vanhoepeni* had the thinnest mean scratch width (2.0 μm) and is closest to *R. darti* and *P. braini* in this regard.

Statistical analysis showed significant variation among the taxa for scratch width (Table 4) and pairwise comparisons indicated that some species were significantly different from one another (Appendix A). The mean scratch widths of *G. vanhoepeni* and *R. darti* were significantly smaller than a number of the compared taxa, including the browser *T. strepsiceros*, the mixed feeders *T. scriptus* and *A. melampus*, and grazer *C. taurinus*.

6.4. Striation orientation concentration (r)

Within-species variation for feature orientation concentration was high and mean values were similar for many of the taxa (Fig. 6). Nevertheless, most of the extant taxa had fairly homogeneously oriented microwear features. For example, the extant grazers ranged from $r=0.60$ to $r=0.74$. The most obvious exception to relatively high mean orientation concentrations was *Litocranius walleri* ($r=0.32$) with a much lower mean value than all other taxa. Most of the extinct taxa had extreme within-species variation. Both *P. braini* and *G. vanhoepeni* had noticeably lower mean values than did the extant taxa.

Table 4
One-way analysis of variance results for microwear features

Feature effect	Sum-of-squares	*df*	Mean-square	*F*	*P*
Pit percentage					
Taxon	172,648.963	16	10,790.560	21.958	0.000
Error	60,935.037	124	491.412		
Pit width					
Taxon	92,706.181	16	5794.136	5.102	0.000
Error	140,808.319	124	1135.551		
Scratch width					
Taxon	92,253.749	16	5765.859	5.061	0.000
Error	141,267.251	124	938.973		
Long axis orientation concentration (*r*)					
Taxon	117,150.809	16	7321.926	7.798	0.000
Error	116,432.691	124	938.973		
Minor axis					
Taxon	136,067.003	16	8504.188	10.819	0.000
Error	97,465.997	124	786.016		
Major axis					
Taxon	162,480.336	16	10,155.021	17.709	0.000
Error	71,108.164	124	573.453		

Statistical analysis confirmed significant variation among the taxa (Table 4). Subsequent pairwise comparisons indicated those taxa that were significantly different from each other (Appendix A). While *P. braini* had a large range in values for this feature, its overall mean ($r=0.49$) was significantly different from *Oryx gazella* (0.74). Similarly, *G. vanhoepeni* had a mean ($r=0.47$) for this feature that was significantly lower when compared to three extant mixed feeders (*T. scriptus*, *O. gazella* and *A. melampus*), two grazers (*H. niger* and *C. taurinus*), and the extinct *R. darti*.

6.5. Overall feature dimensions

The combination of major and minor axes defines the shape of a feature. When these are considered together, MANOVA results indicated significant variation in the model (Table 3). Subsequent ANOVAs on minor and major axes confirmed that significant variation exist for both of these dimensions (Table 4). Post hoc pairwise comparisons revealed the sources of significant differences among the taxa (Appendix A).

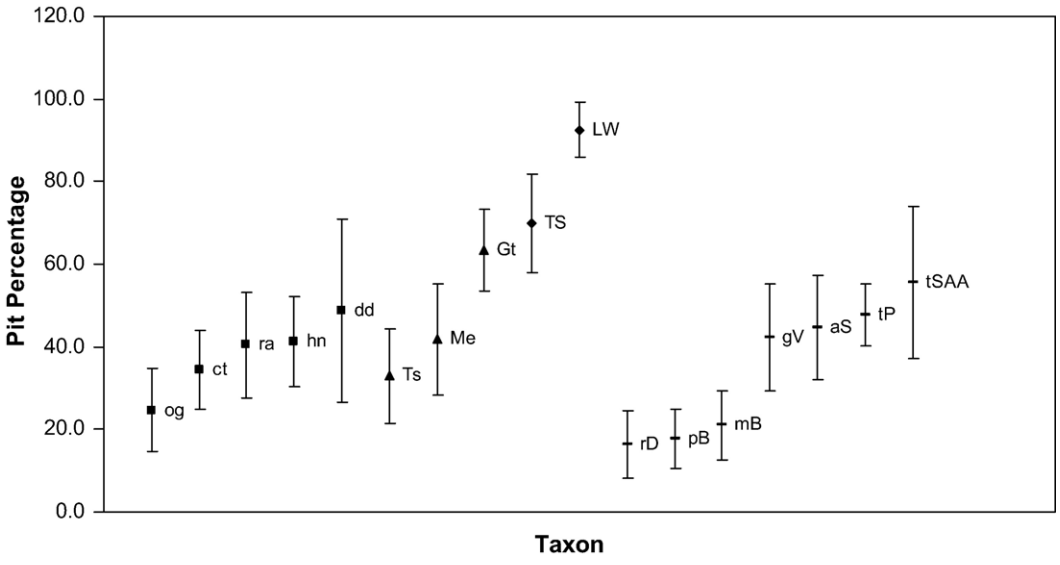

Fig. 3. Pit percentages. Black shapes indicate mean values and vertical lines denote 1 standard deviation. ■=grazer, ▲=mixed feeder, ♦=browser, ━=Makapansgat fossil bovids (taxon codes as in Tables 1 and 2).

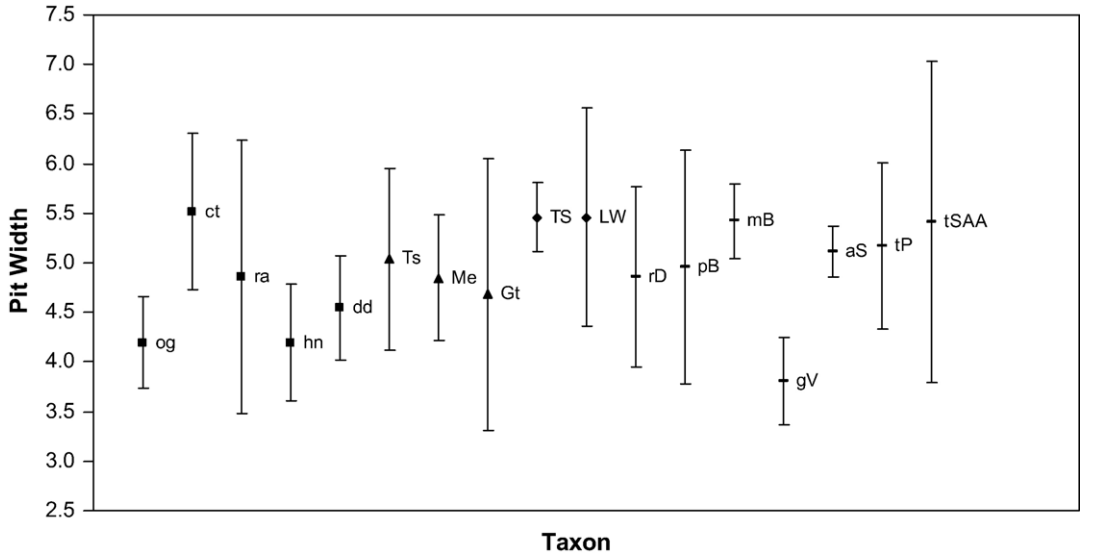

Fig. 4. Pit width. Black shapes indicate mean values and vertical lines denote 1 standard deviation. Dimensions are in μm. ■=grazer, ▲=mixed feeder, ◆=browser, ━=Makapansgat fossil bovids (taxon codes as in Tables 1 and 2).

6.6. Minor axis comparisons

Minor axis means for all taxa ranged from 2.8 to 4.8 μm (Fig. 7). The extant grazer, *Connochaetes taurinus*, tended to have longer minor axes than the *Oryx gazella*. The two extant browsers, *Litocranius walleri* and *Tragelaphus strepsiceros*, generally had longer minor axes compared to other taxa. The Makapansgat bovids, *Redunca darti*, *Parmularius braini*, and *Gazella vanhoepeni* appeared to have similar relatively short minor axis lengths, separating them from *Aepyceros* sp., *Tragelaphus pricei*, and *T.* sp. aff. *T. angasii*, which have longer minor axes on average than all compared taxa except the two browsers.

Statistical analysis confirmed significant variation among the samples analyzed (Table 4) and pairwise comparisons indicated significant differences between the taxa (Appendix A). This confirmed that *C. taurinus* had significantly longer minor axes on average compared to *Oryx gazella*. The only significant difference in the extant

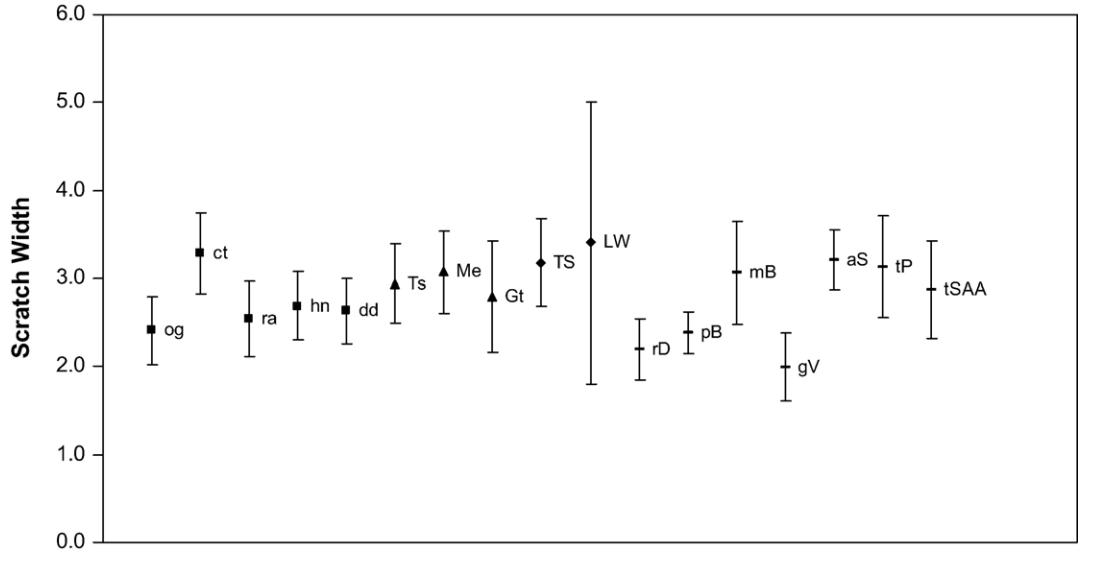

Fig. 5. Scratch width. Black shapes indicate mean values and vertical lines denote 1 standard deviation. Dimensions are in μm. ■=grazer, ▲=mixed feeder, ◆=browser, ━=Makapansgat fossil bovids (taxon codes as in Tables 1 and 2).

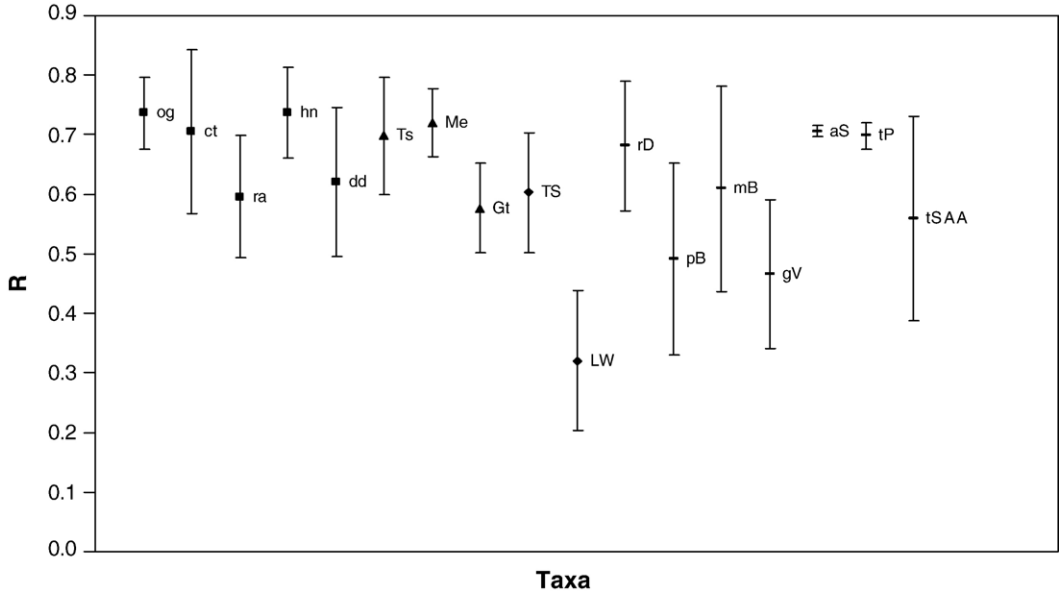

Fig. 6. Striation orientation concentration (*r*). Black shapes indicate mean values and vertical lines denote 1 standard deviation. ■=grazer, ▲=mixed feeder, ◆=browser, ━=Makapansgat fossil bovids (taxon codes as in Tables 1 and 2).

browser and mixed feeder category was between *Tragelaphus scriptus* and *T. strepsiceros*, with *T. scriptus* having much thinner features (for example, see Fig. 2). When all extant species were compared *Oryx gazella* was also significantly different from both browsers and two of the mixed feeders (*Aepyceros melampus* and *Gazella thomsoni*), having a lower mean value for minor axis length.

Significant differences for the fossil taxa were also numerous. *Tragelaphus* sp. aff. *T. angasii* and *T. pricei* have significantly wider features then *R. darti*, *P. braini*, *G. vanhoepeni*, and the extant *O. gazella*. In addition, *R. darti* and *G. vanhoepeni* have significantly thinner features than the two extant browsers, three extant mixed feeders, and *Connochaetes taurinus*. Similarly, *P. braini* has significantly thinner features than the two extant browsers and *C. taurinus*, and *Makapania broomi* has significantly thinner features than *Tragelaphus strepsiceros*.

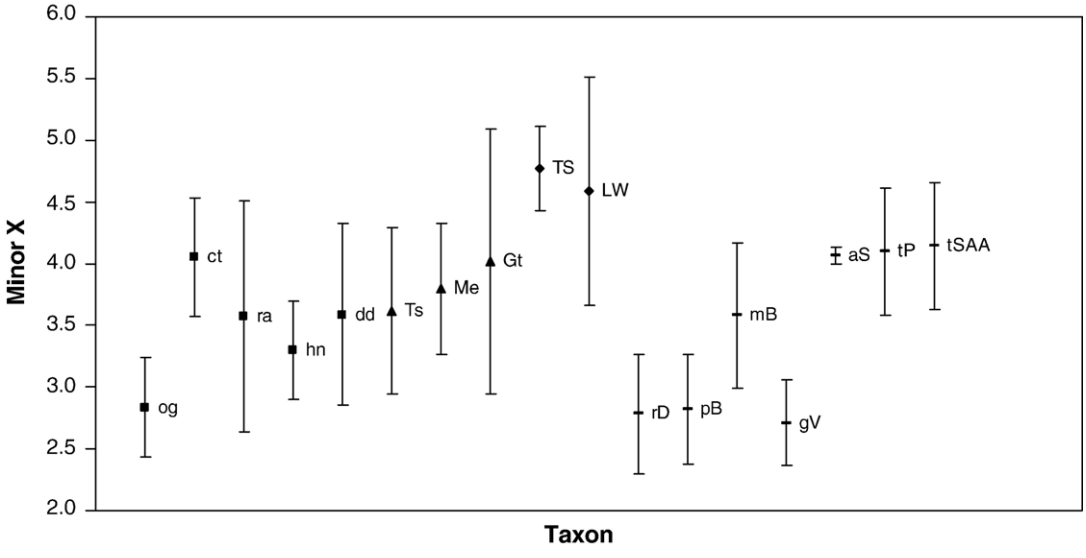

Fig. 7. Minor axis. Black shapes indicate mean values and vertical lines denote 1 standard deviation. Dimensions are in μm. ■=grazer, ▲=mixed feeder, ◆=browser, ━=Makapansgat fossil bovids (taxon codes as in Tables 1 and 2).

6.7. Major axis comparisons

The taxa varied considerably for the mean lengths of the major axis too (Fig. 8). Means for all taxa ranged from 10.0 to 48.4 μm. These values are underestimates because feature lengths were often truncated by the edge of the field of view. However, the results are still comparable between taxa since the same bias (an underestimate in feature lengths) was applied to all the specimens. Obvious differences between the extant taxa are the shorter major axes for the browsers and *G. thomsoni*, particularly when compared to *O. gazella*. The mean major axis values for the extinct taxa separated them into two groups: (1) *Redunca darti*, *P. braini*, and *M. broomi* have longer features, while (2) *G. vanhoepeni*, *Aepyceros* sp., *T. pricei*, and *T.* sp. aff. *angasii* have shorter features.

Statistical analysis confirmed significant variation in this feature (Table 4). Post hoc pairwise comparisons further indicate separation of most taxa by mean major axis length values (Appendix A). Some of the more notable differences in the extant taxa are the significant difference in length between all of the grazers and *Litocranius walleri*, the latter having shorter major axis lengths. The browser, *T. strepsiceros*, only differs significantly from one species at the grazing end of the spectrum, *O. gazella*.

Significant differences were also seen in the extinct taxa. These clearly separate into two groups (Fig. 8), (1) *R. darti, P. braini*, and *M. broomi*, and (2) the other four. The average length of the major axis for *Makapania broomi* is the longest when compared to all the other taxa and it is significantly different from *G. vanhoepeni*, *T. pricei*, and *T.* sp. aff. *T. angasii*. In the same regard *R. darti* is significantly different from *T. pricei* and *G. vanhoepeni*, while *P. braini* is only significantly different from *G. vanhoepeni*.

6.8. General shape comparisons

Fig. 9 shows clear separation in extant grazers and extant browsers based on the means of overall feature shape. As noted above many of the taxa are significantly different from one another. Browsers tend to have short and wide features while grazers have longer and thinner features. For the most part the mixed feeders clump together in the middle. In the extinct taxa there are two primary groupings, one that clusters with grazers (*Makapania broomi*, *Redunca darti*, and *Parmularius braini*) and another that groups near the browsers (*Aepyceros* sp., *Tragelaphus pricei*, *T.* sp. aff. *T. angasii*). *Gazella vanhoepeni* does not group with any of the taxa and is characterized as having relatively short and thin features.

7. Discussion and interpretation of results

Microwear results presented here indicate that extant bovids differ in the patterning of microscopic features on the occlusal surfaces of their teeth, which reflect dietary differences in the taxa. The extinct bovids from Makapansgat differ in their microwear features to the

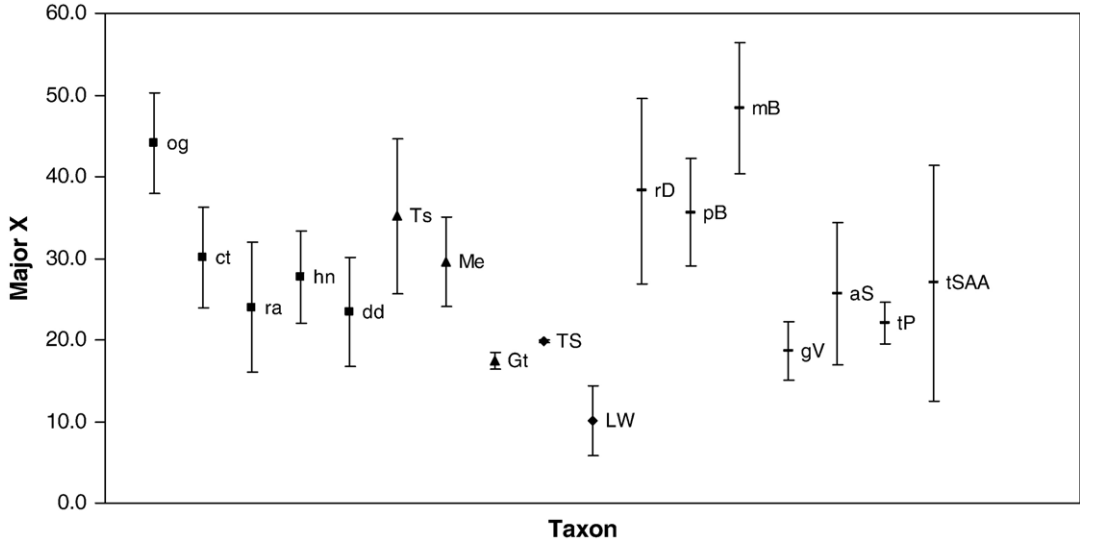

Fig. 8. Major axis. Black shapes indicate mean values and vertical lines denote 1 standard deviation. Dimensions are in μm. ■=grazer, ▲=mixed feeder, ◆=browser, ━=Makapansgat fossil bovids (taxon codes as in Tables 1 and 2).

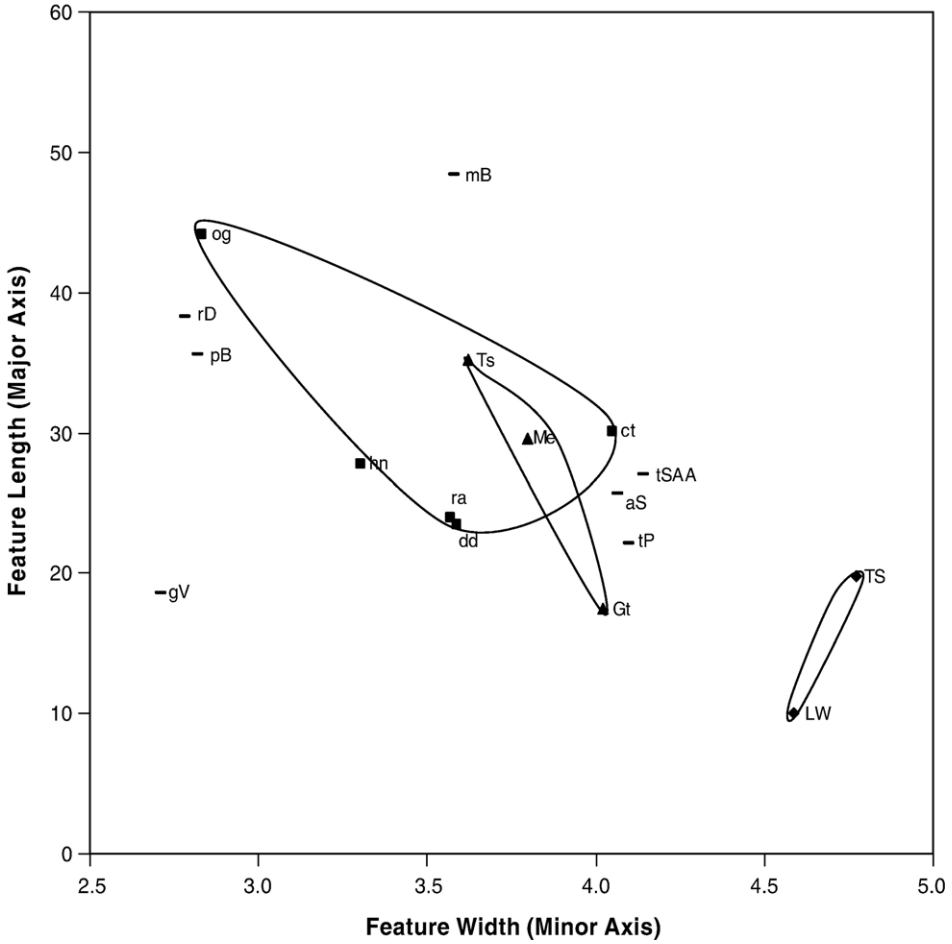

Fig. 9. Bivariate plot of overall feature dimension means. Feature lengths are presented along the *Y*-axis and feature widths are on the *X*-axis. Dimensions are in μm. ■ = grazer, ▲ = mixed feeder, ♦ = browser, ━ = Makapansgat fossil bovids (taxon codes as in Tables 1 and 2). Outlines enclose extant taxa into three dietary groups, grazers, mixed feeders, and browsers.

same degree as the extants. This presumably reflects similar dietary differences in these taxa.

7.1. Pit percentage

7.1.1. Extant taxa

As with previous microwear studies, the percentage of pits separated the extant taxa into dietary categories with browsers having a higher percentage of pits than grazers and mixed feeders overlapping in their pit percentage with either grazers or browsers (e.g., Solounias and Hayek, 1993; Solounias and Semprebon, 2002; Merceron et al., 2004a,b) (Fig. 3).

Litocranius walleri provided the most extreme example of high pit percentage. The shearing facets are covered in pits and have a very low number of scratches (for example see Fig. 2). Others have noted this unique pattern in the gerenuk and have attributed it to their dietary specialization on leaves, shoots, and flowers (e.g., Merceron et al., 2004a). The predominance of small pits on most of the analyzed specimens may demonstrate prism fracturing due to excessive tooth–tooth contact (Teaford and Runestad, 1992). The pit percentage average for *Tragelaphus strepsiceros* is more in-line with that of other typical browsers. These pit percentage values likely reflect the species more generalized browsing diet which includes fruits, flowers, tubers, leaves of many kinds, succulents, and herbs (Estes, 1991).

The extant grazers share a relatively low percentage of pits (or high percentage of scratches). This is expected for species that have high abrasion. This abrasion evidently results from diets that consist predominantly of grasses, which contain a high concentration of silica phytoliths (McNaughton et al., 1985). Of the extant grazers, *Damaliscus dorcas phillipsi* had the highest average and widest range of

mean values for pit percentage. The blesbok is considered to be a relatively pure grazer (Estes, 1991). However, that *Damaliscus dorcas* had the highest pit % of the grazers and *Oryx gazella* had the lowest may seem counter intuitive. The oryx is essentially a grazer but when grass is sparse it includes browse in its diet, and even digs for tubers. With these browsing and digging characteristics one might expect oryx teeth to have higher pit percentages than more typical grazers. However, this apparent anomaly may be explained by the oryx eating arid desert grasses where dust is more prevalent. Such dust covered grasses would result in more extreme abrasion and lower pit percentages. This hypothesis needs further testing and comparison with desert adapted grazers.

Within the mixed-feeding category *Tragelaphus scriptus* produced pit percentage results that deserve discussion. This species is traditionally considered to be a browser (Estes, 1991; Gagnon and Chew, 2000). However, many researchers now consider it to be a seasonal–regional mixed feeder (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Merceron et al., 2004a), and this interpretation is followed here. Merceron et al. (2004a) demonstrated that microwear features could be used to differentiate whether or not a bushbuck specimen was in a grazing or browsing phase. Based on this, the relatively low pit percentage for the bushbucks in the current study might suggest that these specimens were in a grazing phase. However, it should be noted that isotopic data of numerous *T. scriptus* specimens support a C_3 based diet (Sponheimer et al., 2003; Cerling et al., 2003). Thus, extensive C_4 grazing appears to be out of the question in this taxon. While C_3 grazing may explain the enigma, this question needs to be more thoroughly tested by comparing microwear to direct observational data (such as stomach contents) of the same specimens.

7.1.2. Extinct taxa

The extinct Makapansgat bovids clearly fall into two pit percentage groups with statistically significant differences. Based on the placement of *R. darti*, *P. braini*, and *M. broomi* in Fig. 3 these three fossil taxa are considered to be most like grazers. The four other taxa (*G. vanhoepeni*, *Aepyceros* sp., *Tragelaphus pricei*, and *T.* sp. aff. *T. angasii*) fall in the grazing or mixed feeding range. The results for the latter four taxa are in contradiction to other dietary proxy measures that classify these species as browsers (Sponheimer et al., 1999).

Identifying microwear features is subjective, and as Teaford noted "when in doubt throw it out" (Teaford, 1988b). Because many fossils are taphonomically altered to some degree, one has to be careful about what to count. The "off-set" in pit % in the extinct Makapansgat bovids may be the result of two factors, (1) the systematic exclusion of irregular suspicious looking pits, and (2) the tendency for features to become obliterated to some degree through taphonomic processes (King et al., 1999). Scratches are linear features that are readily identifiable and are not easily replicated by naturally occurring taphonomic pathways. However, pit-like features are more difficult to distinguish as antemortem because a number of taphonomic processes produce similar features (King et al., 1999). Thus, the grouping of *G. vanhoepeni*, *Aepyceros* sp., *T. pricei*, and *T.* sp. aff. *T. angasii* with extant grazers and mixed feeders based on pit percentage is probably a taphonomic artifact and observer bias.

If indeed there is an "off-set" in the pit % of fossil bovids compared to the extant taxa, an adjustment might provide a closer approximation to actual diet in the fossil forms. For example, if *Redunca arundinum* and *R. darti* are considered to have similar diets and all the fossil taxa are adjusted the same degree, then *R. darti*, *P. braini*, and *M. broomi* have pit percentages that still overlap with the grazers and *G. vanhoepeni*, *Aepyceros* sp., *Tragelaphus pricei*, and *T.* sp. aff. *T. angasii* would fall into the browser category.

7.2. Pit width and scratch width

7.2.1. Extant taxa

The mean pit and scratch widths of extant bovids did not vary considerably between species, and within-species variation was relatively high for most of the taxa. This may be interpreted as an overall similarity in the size or shape of most abrasive materials eaten by these bovids and/or the response of enamel to abrasives (Ungar, 1995; Ungar and Teaford, 1996). However, there are a couple of taxa that stand out as not following the norm. The significantly wider pits and scratches in *Connochaetes taurinus* clearly separated it from other grazers. This species bulk feeds on short grasses (Estes, 1991; Kingdon, 1997). Thus these features may reflect endogenous silicates in the low grasses and/or grit accumulation on these grasses.

7.2.2. Extinct taxa

The relatively low mean pit and scratch widths of *Gazella vanhoepeni* compared to all other taxa may also be of interest. If it was a mixed feeder like its extant congener *G. thomsoni*, the values are not surprising. However, if it was a browser (as has been suggested by Sponheimer et al., 1999), this combination of thin pits

and scratches may be indicative of a type of browsing that is not recorded here by the extant baseline taxa.

7.3. Striation orientation concentration (r)

The orientation of striations have been used to predict the direction of movement of mammalian teeth in relation to one another since Butler's (1952) and Mills' (1967) original studies in this area. Even at low magnification it is apparent that some bovids, particularly grazers, have scratches that run parallel to one another on their shearing facets. These features run perpendicular to the long axis of the tooth and reflect the lateral movement of the jaw in chewing.

Both Grine (1986) and Van Valkenburgh et al. (1990) suggested that uniform parallel striations on enamel may be indicative of foods that allowed more precise jaw motion in mastication, while striations that are more heterogeneous were the result of eating foods that caused more eccentric jaw motion. Both of these patterns are evident in the extant bovids analyzed here.

7.3.1. Extant taxa

Extant grazers had high striation orientation concentrations, which probably reflect their diet of grass (considered to be a soft and tough food) and the phytoliths in the grass. However, the greater kudu (*T. strepsiceros*) also had a relatively high striation orientation concentration though it is a browser with a diet that ranges from fruits, to leaves, to minimal amounts of new grass. Striation orientation concentration is based on the long axis measurement, thus it considers all features (not just scratches). Although *T. strepsiceros* has a relatively high pit percentage, and is certainly a browser, the high striation orientation concentration in this species is not surprising. These results may indicate that many of the kudu's preferred foods contain hard objects (such as grit or phytoliths) that are dragged across the teeth in a consistent pattern. The gerenuk has a rather unique diet and has a particularly low striation orientation concentration. It feeds almost exclusively on the flowers, leaves, and shoots of shrubs and trees (Estes, 1991). Because of their diameter, shoots cause eccentric motion in the jaw when chewing. Thus, low striation orientation concentration makes sense for the gerenuk because its diet is low in silica phytoliths and contains food items that cause considerable motion of the jaws.

7.3.2. Extinct taxa

Most of the extinct taxa show extreme within-species variation for striation orientation concentration making the results difficult to interpret. However, *Redunca darti* and *Gazella vanhoepeni* are significantly different from one other. Based on comparisons with the extants, *R. darti* most likely had a diet that contained small hard particles (such as grasses and silica phytoliths) that were ground across the teeth in a consistent manner. This is the typical grazing pattern. In contrast, *G. vanhoepeni* had a significantly lower striation orientation concentration, suggesting a greater deal of eccentric movement in mastication. A pattern that is typical of browsers.

7.4. Overall feature dimensions

As noted by Ungar (1996), the similarities between pit percentage results and a bivariate analysis of overall features suggests that the latter type of analysis may have similar dietary implications to pit:scratch ratios. The advantage to the bivariate analysis based on overall feature dimensions is that the results do not depend on an arbitrary pit percentage ratio to separate features into subjective categories (Ungar, 1996).

7.4.1. Extant taxa

Feature dimension results for the extant bovids (Fig. 9) were similar to that of pit percentage and separated the taxa into two clear groups, browsers with wider and shorter features, and grazers with thinner and longer features. Overall, the bivariate analysis does a better job at categorizing the taxa because it provides a continuum of feature shape that allows more distinct separations. For example, the bivariate analysis clearly shows that *Oryx gazella* tends to have longer and thinner features when compared to *Connochaetes taurinus* while *Hippotragus niger* and *C. taurinus* have similar average feature lengths but *C. taurinus* tends to have wider features.

7.4.2. Extinct taxa

The bivariate plot of feature dimensions separates the extinct taxa into two primary groups (Fig. 9). One of the groups on the bivariate plot is composed of *Redunca darti*, *Parmularius braini*, and *Makapania broomi*. This is the grazing end of the spectrum. The other group, *Tragelaphus pricei*, *T.* sp. aff. *T. angasii*, and *Aepyceros* sp. fall between the grazers and browsers, yet these three taxa are considered to be browsers based on other proxy measures (Sponheimer et al., 1999). Their location on the bivariate plot certainly does not exclude them from being browsers as only two extant browsers were included in the comparison. However, as was noted in the discussion on pit percentage there is likely an "offset" for pit-like features in the extinct taxa. Taking this

into consideration only a slight adjustment would be needed to place these three fossil taxa closer to the extant browsers.

One of the most interesting differences revealed by the bivariate plot is the difference between *Gazella vanhoepeni*, the two *Tragelaphus* taxa, and *Aepyceros* sp. All four of these group together in terms of pit percentage but the bivariate analysis reveals a dramatic difference in the shape of features. If indeed *G. vanhoepeni* was a browser (as has been suggested by Sponheimer et al., 1999), its consistently short and thin features suggest it was doing something quite different than the other browsers in this study.

7.5. Summary of results

Microwear data correctly sorted a baseline series of extant bovids into their proper dietary categories. In addition, this analysis pointed out subtle differences that relate to the material properties and abrasive characteristics of preferred foods. For example, the shoots and leaves that make up the diet of the browsing gerenuk result in a high percentage of pits, relatively wide and long features, and a low striation orientation concentration. In contrast, the close cropping of short grasses in the grazing wildebeest results in a low percentage of pits, wide and medium length striations, and a high striation orientation concentration.

Analysis of the same features in the extinct bovids of Makapansgat provides evidence of the types of foods eaten by these taxa and separates them into at least two dietary groupings. Based on these results, *Parmularius braini*, *Redunca darti*, and *Makapania broomi* consistently group with extant grazers in their microwear features, suggesting this was the overall diet of these bovids. The degree of separation between this group and the second group (which contains *Tragelaphus pricei*, *T.* sp. aff. *angasii*, and *Aepyceros* sp.) is significant and suggests different diets between these two groups.

However, direct comparison of this second group to the extant bovids does not clearly resolve them into the expected dietary category of browser (based on isotopic results). This is probably the result of exclusion of questionable corroded pit-like features in the fossil specimens during the digitizing. Thus there is likely an "off-set" for the fossil taxa, particularly browser types, when compared to the extants. *Gazella vanhoepeni* also groups with *T. pricei*, *T.* sp. aff. *T. angasii*, and *Aepyceros* sp. in terms of pit percentage and a similar bias may have affected its results. However, *G. vanhoepeni* was also unique among the data set suggesting it had a diet unlike all of the compared taxa.

8. Summary and conclusions

8.1. Comparing dietary proxy measures

The paleodiets of seven Makapansgat bovids have now been analyzed using five different proxy measures. These dietary reconstructions are compared below. Table 5 summarizes the paleodietary interpretations.

8.1.1. Gazella vanhoepeni

Taxonomic uniformitarianism places *G. vanhoepeni* as a mixed feeder, while ecomorphology suggests a mixed feeder preferring browse. Stable carbon isotope analysis however indicates it had a C_3 diet and this was interpreted as evidence of a browsing diet (Sponheimer et al., 1999). However, the mesowear data suggests it was a mixed feeder (Schubert, in press). One possibility for the discrepancy between the mesowear and isotopic data is that *G. vanhoepeni* was incorporating C_3 grass into its diet, a scenario that would raise $\delta^{13}C$ values while at the same time offsetting the abrasion/attrition wear gradient towards the abrasion end of the spectrum. Sponheimer et al. (1999) reject the idea of C_3 grazing in this taxon, suggesting that if this were the case other taxa should have skewed $\delta^{13}C$ values. The microwear results suggest a unique diet when compared to the extant baseline and the other Makapansgat bovids. Species that feed on C_3 grasses tend to have wear facets that are dominated by elongated thin features (Solounias and Semprebon, 2002; Merceron et al., 2004a). This was not the case in *G. vanhoepeni*, which is characterized by thin but relatively short microwear features. One possibility is that *G. vanhoepeni* had a browsing diet (based on isotopes) that contained an abrasive component (based on mesowear) that differed from the extant browsers. An alternative hypothesis is that the diet of *G. vanhoepeni* did include C_3 grasses that were not incorporated into the diet of other extinct taxa, and the range of microwear features caused by C_3 grasses have not been fully demonstrated. Because of these uncertainties, *G. vanhoepeni* is considered to be either a browser or a mixed-feeder preferring browse.

8.1.2. Redunca darti

Ecomorphological data and taxonomic uniformitarianism suggest that *Redunca darti* was a fresh grass grazer. Stable carbon isotope analysis places it as a grazer (Sponheimer et al., 1999). Sponheimer et al. (1999) interpret the morphological data as being

Table 5
Dietary reconstruction of the Makapansgat bovids using taxonomic uniformitarianism, ecomorphology, stable carbon isotopes, microwear, and mesowear

Taxon	Taxonomy	Ecomorphology	Isotopes	Mesowear	Microwear	Final
Tragelaphus sp. aff. *T. angasii*	B	B	B	B	MF-B or B	B
Tragelaphus pricei	B	B	B	B	MF-B or B	B
Redunca darti	FG	FG	G	G	G	FG or G
Gazella vanhoepeni	MF-?	MF-B	B	MF	MF-B or B	MF-B or B
Aepyceros sp.	MF-G	MF-G	B	B	MF-B or B	B
Parmularius braini	G	MF-G	G	G	G	G
Makapania broomi	MF-?	MF-G	MF-G	G	G	MF-G or G

The last column combines methods taking into consideration the strengths and weaknesses of the proxy measures. Diets: FG=fresh grass grazer; G=grazer; B=browser; MF-G=mixed feeder preferring graze; MF-B=mixed feeder preferring browse.

indicative of a fresh grass grazer and mesowear (Schubert, in press) and microwear group it most closely with grazers. While all of the proxy measures here are in agreement and categorize this species as a grazer, microwear and mesowear do not group it with extant fresh grass grazers. Based on these results *R. darti* is identified as either a generalized grazer or a fresh grass grazer.

8.1.3. *Parmularius braini*

Taxonomic uniformitarianism predicts that *P. braini* was a grazer, and ecomorphological data was interpreted as suggesting a mixed feeder preferring grass (Reed, 1996; Sponheimer et al., 1999). Stable carbon isotopes support a grazing reconstruction (Sponheimer et al., 1999) and microwear agrees with this assignment. Mesowear analysis supports these reconstructions, and further, places it in an extreme grazer category (Schubert, in press).

8.1.4. *Aepyceros sp.*

Taxonomic uniformitarianism and ecomorphology suggest that *Aepyceros* should be a mixed feeder preferring grass. However, Sponheimer et al. (1999) found that this taxon had a pure C_3 diet and thus classified it as a browser. Mesowear is in agreement with the carbon isotope data, classifying *Aepyceros* sp. as a browser (Schubert, in press). In the microwear analysis only two specimens were analyzed, thus the sample was too small to be statistically significant. However, microwear results on these two specimens grouped this specimen most closely to *T. pricei* and *T.* sp. aff *T. angasii*, both of which are considered to be browsers based on other dietary proxy measures. *Aepyceros* sp. is classified here as a browser.

8.1.5. *Tragelaphus sp. aff. T. angasii*

Taxonomic uniformitarianism, ecomorphology, stable carbon isotopes (Sponheimer et al., 1999) and mesowear (Schubert, in press) data suggest that *Tragelaphus* sp. aff. *T. angasii* was a browser. Microwear results for *T.* sp. aff. *T. angasii* were very similar to that of *T. pricei* and *Aepyceros* sp., suggesting that these three taxa had similar diets. While a browsing diet was not confirmed based on microwear results, it was not rejected either. The final classification of *T.* sp. aff. *T. angasii* is browser.

8.1.6. *Tragelaphus pricei*

This species had nearly identical microwear results to *T.* sp. aff. *T. angasii* and thus the indeterminate interpretation is the same. It is considered to be a browser based on taxonomic uniformitarianism, ecomorphology, stable carbon isotopes (Sponheimer et al., 1999) and mesowear (Schubert, in press).

8.1.7. *Makapania broomi*

Taxonomic uniformitarianism places *M. broomi* as a mixed feeder while ecomorphology and stable carbon isotopes put it in a mixed feeder preferring grass category (Sponheimer et al., 1999). Both mesowear (Schubert, in press) and microwear group *M. broomi* most closely with grazers. This does not differ dramatically from interpretations based on stable carbon isotope data, since the $\delta^{13}C$ values come very close to placing this species with grazers. Undoubtedly *M. broomi* had an abrasive diet composed of a high percentage of C_4 grasses. Based on these results its final dietary classification is grazer or mixed feeder preferring grass.

8.2. Implications for the paleoenvironment of Makapansgat

In the interdisciplinary study of Makapansgat bovid diets by Sponheimer et al. (1999), the intention was not to offer yet another environmental interpretation of the Makapansgat Member 3 fauna, but to compare the results of different dietary proxy measures and test taxonomic

uniformitarianism. Like Sponheimer et al. (1999), the current study focuses on comparing techniques and refining paleodietary interpretations that are used for environmental reconstructions. The microwear results presented here represent a step towards better understanding the diet and thus habitat of selected extinct bovids, taxa that have been extensively used in the environmental reconstruction of Makapansgat and other sites. This study makes it clear that interdisciplinary paleodietary research is needed if we are to continue using fossil taxa like bovids as indicators of past environments.

So, what can be said about the paleoenvironment of the Makapansgat Member 3 fauna based on the new data presented here? The carbon isotope data (Sponheimer et al., 1999), mesowear (Schubert, in press) and microwear indicate a stronger browsing component than either taxonomic uniformitarianism or ecomorphology. However, this does not change Reed's (1996, 1998) paleoenvironmental reconstruction of the site as a "bush and woodland habitat" based on ecomorphology because browsers tend to prefer these types of environments. Thus, the revised classifications strengthen Reed's original interpretation.

8.3. Summary

1) Microwear results separated an extant baseline series of bovid taxa into grazers and browsers. As with previous microwear studies, mixed feeders overlapped with results for the browsing and grazing species. Extinct taxa clearly fell into two groups with the same degree of separation as the extant grazers and browsers. Microwear classified the same taxa as grazers as the isotopic and mesowear analyses. Adjusting for pit shift *Gazella vanhoepeni*, *Aepyceros* sp., *Tragelaphus* sp. aff. *T. angasii*, and *T. pricei* group with browsers. This agrees with the mesowear (except for *G. vanhoepeni*) and isotopic data.
2) The addition of microwear analysis to these bovid taxa refined their dietary classifications. These results suggest that nongenetic paleodietary signals are needed to accurately reconstruct past diets and habitats. For example, microwear agrees with other nongenetic proxy measures, such as mesowear and isotopes, which indicate the fossil *Aepyceros* sp. was a browser and not a mixed feeder like its morphologically similar modern counterpart the impala, *A. melampus*. Further, microwear demonstrated that *Gazella vanhoepeni* has unique microwear features. Based on all the nongenetic data it was a mixed-feeder preferring browse or a browser.
3) The four methods presented here provide a temporal continuum, with genetic signals such as ecomorphology indicating behavioral adaptations over long periods of time, mesowear and stable carbon isotopes reflecting different aspects of diet from months to years of an animal's lifetime, and dental microwear providing a snapshot of an animal's diet. This study pointed out that multidisciplinary paleodietary studies that include nongenetic and phylogenetic signals can lead to a better understanding of the paleodiets of taxa and the range of possible diets in lineages through time.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2006.04.004.

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